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Chapter 11

Ozone Exposure-Based Growth Response Models for Trembling Aspen and White Birch

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Abstract

We developed free-air exposure regression-based models comprising annual growing season 4th highest daily maximum 8-h average ozone (O_3) concentration, growing degree days (GDD), and average wind speed (WS). The models include 95% confidence bands for determining uncertainty of prediction. The models are statistically significant, provide a high goodness of fit, and can be used within the ambient air context. Trembling aspen (*Populus tremuloides*) clones 216, 42E, 271, and 259 responded negatively to O_3. Aspen clone 8L responded positively to growing season 4th highest daily maximum 8-h average O_3 concentration ≤ 90 ppb. White birch (*Betula papyrifera*) responded positively to growing season 4th highest daily maximum 8-h average O_3 concentration <80 ppb and negatively at higher concentrations. These responses conform to the toxicological response concept of hormesis. Regression analysis demonstrated that annual growing season 4th highest daily maximum 8-h average O_3 concentration performed much better as a single O_3 exposure index for trembling aspen and white birch cross-sectional area growth than did W126, SUM06, AOT40, and maximum 1-h average O_3 concentration. Growing season 4th highest daily maximum 8-h average O_3 concentration is most closely associated with the actual measured response in the biological endpoint. The W126 index significantly overestimated the negative growth response of aspen and birch to O_3. The growing season 4th highest daily maximum 8-h average O_3 concentration, cumulative GDD, and average WS-based model may provide an underutilized opportunity for scientifically defensible risk analysis within the North American air quality context.

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11.1. Introduction

11.1.1. Ozone, forests, and risk analysis

Over the past 50 years, a large volume of literature has documented ozone (O_3) impacts on forest trees (see reviews by Ashmore, 2004; Bytnerowicz et al., 2003; Chappelka & Samuelson, 1998; Karnosky et al., 2007a; Kickert & Krupa, 1990; McLaughlin & Percy, 1999; Percy et al., 2003). Ozone effects are known to cascade through tree gene expression, biochemistry, and physiology, ultimately feeding back to productivity, predisposing trees to pest attack and causing changes in water-use efficiency (Karnosky et al., 2003c, 2005; Percy et al., 2002). Recent long-term, free-air investigations have confirmed earlier findings on productivity loss under O_3, but do not provide evidence for altered patterns in allometry or carbon (C) allocation as previously reported in open-top chamber studies (King et al., 2005; Kubiske et al., 2006).

In a retrospective review of the roles of air pollutants and climate in North American forest health, McLaughlin and Percy (1999) reported that O_3 was deleteriously affecting forest ecosystem function across large and geographically widely separated areas of the continent. Ollinger et al. (1997) simulated the effects of O_3 on hardwood forest types in the northeastern U.S. and estimated growth reductions between −3% and −22%. Later, Laurence et al. (2001) linked the mechanistic TREGRO model with the ZELIG stand model, parameterized them with biological and meteorological data from three sites, and simulated 100-year growth under five O_3 exposure regimes. Change in *Pinus taeda* basal area ranged from +44% to −87% depending on O_3 exposure and precipitation, whereas basal area of *Liriodendron tulipifera* (generally considered O_3 sensitive) was not affected. Weinstein et al. (2005) used the same models to simulate growth of *Pinus ponderosa* and *Abies concolor* under increased O_3 exposures in the western San Bernardino and Sierra Nevada mountains. They predicted negative effects on *P. ponderosa* but little response in *A. concolor* due to differential sensitivities to O_3, influences of competition, and soil moisture. Interestingly, simulations by Tingey et al. (2004) were among the first to demonstrate a link between improved emission control strategies and improved tree growth. However, there remain questions as to whether process models can be accurately parameterized to predict mature tree response (Samuelson & Kelly, 2001).

Recently, physiological effects of O_3 and biogeochemical changes have been scaled (Felzer et al., 2004; Ollinger et al., 2002) to the landscape. These models predicted that O_3 levels in the United States could largely offset increased forest productivity caused by increasing atmospheric carbon dioxide (CO_2) concentrations. Although certainly indicating the direction and magnitude of potential impact on forest productivity, these models are built partially on assumptions around linearity of response and O_3 exposure indices that do not perform well within the North American ambient air context (Karnosky et al., 2005; Percy et al., 2006, 2007).

Risk analysis to date has relied, for the most part, on dose–response and mechanistic research in chambered environments that have limited use in terms of extrapolation to risk analysis (Manning, 2005a). One key deficiency, identified earlier by Karnosky et al. (2003a), was the urgent need to couple air quality and meteorology measurements in time and space to effects analyses. There is a clear need for new approaches that can increase scientific certainty in dose–response knowledge so as to bring greater certainty to risk modeling. Importantly, there is a requirement that new approaches demonstrate how they contribute to increased "scientific literacy" (Orbach, 2005), thus enhancing usefulness within the context of ambient air quality management.

11.1.2. Objective

Our objective was to develop O_3 exposure-based trembling aspen (*Populus tremuloides*) and white birch (*Betula papyrifera*) growth response models from 5 years' co-measured indicator-response data. The data used were collected in a free-air exposure system designed to reflect the ambient air quality reality in North America.

11.1.3. Air quality standards to protect forest trees

As summarized in Percy and Karnosky (2007), the best current science, balanced by social, economic, and political considerations, is employed to establish North American ambient air quality standards. The United States and Canada have both established the O_3 air quality standard as "the 3-year average of the annual fourth highest daily maximum 8-h average O_3 concentration" (Canadian Council of Ministers of the Environment (CCME), 2000; US Federal Register, 2008). In the United States, there is a primary standard (human health-based) and a secondary standard (welfare-based) that can be different or the same. A legally binding, primary standard of 75 ppb O_3 is now used for regulatory purposes, with the secondary standard set the same as the primary standard at this time. In Canada, the form and averaging time are the same as in the United States, but the level differs. A Canadian target value of 65 ppb O_3 (human health-based, not legally binding) has been adopted.

Establishing cause–effect relationships for ambient O_3 exposure and tree growth has proved to be an elusive goal (Manning, 2005a), making scaling up to the landscape level difficult (Karnosky et al., 2005). Foley et al. (2003) stated that, for human effects, "Exposure-based metrics provide an information-rich tool in assessing relative effectiveness of alternative control strategies and introduce a higher degree of accountability in meeting NAAQS by augmenting air quality metrics with ones more closely associated with morbidity and mortality caused by air pollution exposure." It is clear from the comprehensive review by Musselman et al. (2006) that, during the past 30 years, hourly averaged O_3 data have been summarized in many different ways to assess risk to vegetation. Among indices receiving the most attention in analyses of exposure–response relationships in chambered studies are: the SUM06 threshold-based sum of daytime O_3 concentrations ≥ 60 ppb (Lefohn & Foley, 1992); the accumulated over a threshold (AOT)-based sum of hours of the day with a clear-sky global radiation above $50\,W\,m^{-2}$ (usually 07:00–21:00 h accumulated over 3 months for crops and 6 months for trees) O_3 concentrations >40 ppb (Fuhrer et al., 1997); and the sigmoidally weighted W126 function (Lefohn & Runeckles, 1987; Lefohn et al., 1988) under previous discussion for potential use in a secondary standard (U.S. Environmental Protection Agency (US EPA), 1996, 2006).

In the specific case of regulating surface-level O_3 to protect vegetation, continued research to define our estimate of the level of exposure that will protect vegetation is still clearly needed (Laurence & Andersen, 2003). Recently, McLaughlin et al. (2007a, 2007b) and McLaughlin and Nosal (2008) have used a field-based open-air approach with electromechanical dendrometer techniques to model specific effects of O_3 in the presence of co-varying influences of other environmental variables important to O_3 flux. Regression coefficients for ambient O_3 exposure (cumulative SUM06) prediction were negative and statistically significant for *Pinus rigida*, *Q. rubra*, *Q. prinus*, and *Carya* spp. Model predictions of growth loss in the range of 50% in high O_3 years agreed well with observed growth. This approach also has great potential for determining the contribution of O_3 to changes measured in tree growth, and for scaling hourly effects of O_3 to cumulative impact over the growing season (McLaughlin et al., 2003).

In reviewing the use of exposure- and flux-based ozone indices for predicting vegetation effects, Musselman et al. (2006) concluded that, at the moment, "… exposure-based metrics appear to be the only practical measure for use in relating ambient air quality standards [in North America] to vegetation response."

11.2. Materials and methods

11.2.1. Analytical approach

Data from the Aspen Free Air Carbon Dioxide Enrichment (FACE) O_3 exposure experiment, where response measurement was tightly coupled with meteorological measurements in both space and time, were used to build a matrix of 30 cases [5 years' data × six FACE rings (three control, three O_3)] for analysis. Each individual case comprised (1) a response variable (mean stem cross-sectional area); (2) an O_3 indictor variable (annual growing season 4th highest daily maximum 8-h O_3 concentration and four other O_3 indices); and (3) meteorological indictor variables important in controlling O_3 flux into plants and ambient O_3 concentrations (Krupa et al., 2003; National Research Council (NRC), 1991).

We tested five aspen clones (total = 1723 trees in 1999) and white birch (total = 222 trees in 1999) covering a range of documented (Karnosky et al., 1996, 2005) sensitivity to O_3. Our O_3 exposure–response models integrated end-of-season growth response over a 5-year growth period (1999–2003). During that time, aspen height (averaged across clones) within the aspen plantation half of the control rings increased from 2.8 m to 5.8 m and the stand reached (2002) canopy closure.

11.2.2. The Aspen FACE experiment

The Aspen FACE experiment (32 ha) is situated on sandy loam glacial outwash soil near Rhinelander, northern Wisconsin, US (45°06′N; 89°07′W; 490 m asl; www.aspenface.mtu.edu, last accessed on July 20, 2008). The experiment consists of a full factorial with 12 30-m diameter FACE rings: three controls, three elevated CO_2, three elevated O_3, and three elevated CO_2+O_3. The rings were planted in 1997 and treatments occurred from bud break to the end of growing season from 1998 to present.

The eastern half of each ring was randomly planted in two-tree plots at 1 m × 1 m with five trembling aspen (*P. tremuloides* Michx.) clones of known and widely varying tolerance to O_3. The northwest quarter was planted with a mixture of aspen (clone 216) and sugar maple (*Acer saccharum* Marsh.). The southwest quarter was planted with a mixture of aspen (clone 216) and a range-wide, northern Lake States source of white birch. Since 2003, Aspen FACE has been a designated component of a distributed U.S. Department of the Environment (US DOE) User Facility. Complete details on baseline site physical and chemical characteristics, micrometeorology measurement, O_3 measurement, selection of plant material, and experiment operation are published elsewhere (Dickson et al., 2000; Karnosky et al., 2003c).

11.2.3. Ozone fumigation

The Aspen FACE protocol for O_3 fumigation prescribed a 07:00–19:00 h (12 h; based on zenith sun angle) daily exposure, 7 days a week from bud break to bud set. Elevated O_3 was controlled so as to track ambient O_3, yielding a repeatable diurnal increase to early afternoon followed by a decrease to late afternoon. Elevated hourly average O_3 concentrations (maximum hourly average concentration achieved 13:00–14:00 h) followed ambient concentrations closely throughout the experiment (Karnosky et al., 2005).

Ozone was not released if leaf surfaces were wet or if daily maximum temperature was predicted to be $<15°C$. In this analysis, using 5 years (1999–2003) of co-measured response-predictor variables, growing seasons ranged from 136 to 144 days. In practice, during 1999–2003, O_3 was fumigated on only 48.7–51.6% of potential growing season days as follows: 1999 (124 d, 820 h); 2000 (121 d, 800 h); 2001 (122 d, 777 h); 2002 (107 d, 787 h); 2003 (117 d, 893 h) (Percy et al., 2006, 2007). Target elevated O_3 was $1.5\times$ (1999) or $1.4\times$ (2000–2003) ambient air.

11.2.4. Response and indictor variables

Building on earlier work (Percy et al., 2006, 2007), the list of O_3 indices tested was expanded to include the W126 index (Lefohn & Runeckles, 1987). The response variable used in this study was aspen clone mean stem cross-sectional area (m^2). End-of-growing season tree diameters were measured at 3 cm (1998–2001) or at 10 cm (2001–2003) above ground. Diameters used for 2001 were the averages at 3 cm and 10 cm as described by Kubiske et al. (2006). All measurements were collected on individual trees growing within the core area (about five rows inward from the free-air inlets toward the ring center). Diameters (dia ± 1 cm) were converted to cross-sectional area using the equation cross-sectional area $(m^2) = 0.00007854 \times (dia^2)$ (Husch et al., 2003). Mean cross-sectional stem area for the five aspen clones and white birch was then calculated for each FACE ring used in this study (three control, three O_3).

Annual growing season 4th highest daily maximum 8-h average hourly O_3 (modified U.S. and Canadian air quality standard metric form and averaging time) was calculated from continuous O_3 monitoring at ring center above the canopy (10 m) for each elevated O_3 ring. Ozone was not continuously monitored within Aspen FACE control rings. Spatial analysis (ESRI ARC™ Map; data interpolated using a tension spline, weight 0.1) was completed for 1999–2003 from 24-h continuous hourly active fence line monitor data collected along the Aspen FACE perimeter fence lines. This analysis showed little within-season variation in growing season 4th highest daily maximum 8-h average hourly O_3 across the site (Percy, unpublished). Therefore, control ring annual 4th highest daily maximum 8-h average hourly O_3 was taken from the published on-site ambient monitor (EPA AIRS ID 550850004420101; data available at http://oaspub.epa.gov/airsdata) and assigned to each control ring.

Meteorological indictor variables were calculated from higher frequency sampling intervals described elsewhere (Dickson et al., 2000). Daytime temperature, solar radiation, wind speed (WS), relative humidity (RH), and precipitation data used in this study were measured at the on-site Aspen FACE 20-m meteorological tower. Growing degree days (GDD) or "heat units" were computed by subtracting a base temperature of 10 °C from the average of the maximum and minimum temperatures (5 min scan interval) for each day measured at 10 m. If the daily average temperature computed from the maximum and minimum temperatures was less than 10 °C, the average temperature was set to 10 °C so that the GDD contribution from that day was zero, and not negative. Accumulated growing season photosynthetically active solar radiation (PAR) ($mmol\,m^{-2}\,s^{-1}$; 5 s scan interval) was calculated as the sum of half-hourly values. Average growing season WS ($m\,s^{-1}$; 5 s scan interval; 30 min average reporting) and average growing season 09:00 h RH (%; 5 min scan interval; 30 min reporting) were calculated from data collected at 10 m. Time-specific growing season precipitation (mm) was calculated from monthly sums at the base of the tower. Average growing season soil moisture content (SMC) (%; 2 h scan interval) was calculated from bi-weekly averages taken at 5–35 cm below the surface within the FACE ring aspen communities.

11.2.5. Statistical analysis

Exploratory statistical analysis included investigation of the relationship between O_3 and mean cross-sectional area growth. Pearson correlation (Millard & Neerchal, 2001) was used to characterize the relationships between the dependent and the seven independent indictor variables. As correlation analysis showed that RH and precipitation were very highly correlated ($r = 0.799$; $p = 0.0000$) and co-linear with respect to other predictors, RH was omitted as a predictor variable in subsequent analyses.

Complete multiple regression (Millard & Neerchal, 2001) models were developed using the remaining six indicators. Analysis of residuals for the 30 cases constructed for each of the five aspen clones and white birch indicated highly standardized residuals for only two observations (2002, O_3 ring 3 and 2003, O_3 ring 3; both clone 8L). These two observations (residuals equal to 0.0010) did not conform to the normal probability plot and were deleted from the analysis.

To determine the most suitable regression models for impact assessment of O_3 and the other indictor variables on cross-sectional area growth, we systematically applied the best regression algorithm (Millard & Neerchal, 2001) to each of the five aspen clones and white birch. Using this outcome, we developed multiple regression models optimizing (minimum number of indictors with highest r^2 adjusted) on the best indictors of aspen cross-sectional area growth.

Confidence intervals were computed using Monte Carlo techniques (Millard & Neerchal, 2001) to randomly generate various scenarios ($n >$ 3000) for all relevant ranges of O_3, GDD, and WS. Normal probability plots for the predictors indicated a perfect fit for their distribution. Resulting confidence (95%) bands in two-dimensional Euclidean spaces were represented by graphs in planes for ease of visualization.

11.3. Results

11.3.1. Five-year trend in indicator variables

Metadata for the indicator variables used in this study are graphed in Fig. 11.1. The growing season 4th highest daily maximum 8-h average O_3 concentration ranged from 94 ppb (elevated O_3 rings 1999) to 65 ppb (control rings 2002). There was no overall trend in cumulative growing season GDD. GDD decreased in the order 2002 > 1999 > 2001 > 2003 > 2000 (Fig. 11.1). Growing seasons 1999 and 2002 were slightly (up to 16%) warmer than 2000, 2001, and 2003. There was a tendency for average growing season WS at Aspen FACE to decrease (except for 2002) over the 5 years. Average WS ranged from 1.18 $m\,s^{-1}$ (1999) to 0.98 $m\,s^{-1}$ (2003) (Fig. 11.1). There was no apparent trend in accumulated growing season PAR, which ranged from 3211.2 $mmol\,m^{-2}\,s^{-1}$ (2001) to

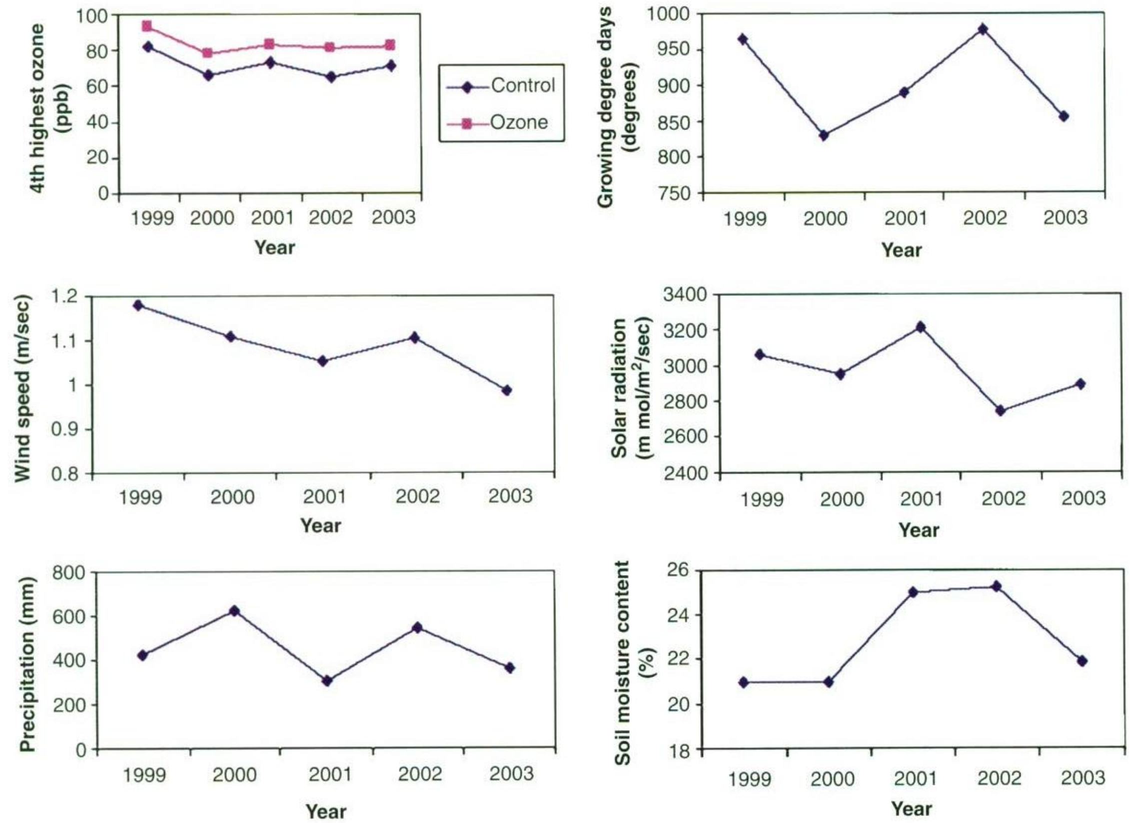

Figure 11.1. Five-year (1999–2003) trends in Aspen FACE annual growing season 4th highest daily maximum 8-h average O_3 concentration (means of three replicate rings), accumulated GDD, average PAR, average WS, total precipitation, and average biweekly SMC.

2735.6 mmol $m^{-2} s^{-1}$ (2002) (Fig. 11.1). Growing season precipitation alternated (52% maximum change) biannually between lower amounts (1999, 425.11 mm; 2001, 301.86 mm; 2003, 358.14 mm) and higher amounts (2000, 625.69 mm; 2002, 547.57 mm) (Fig. 11.1). Average growing season SMC beneath the aspen stands varied little during 1999–2003 and ranged from 19.42% (elevated O_3 ring 1,3 in 1999) to 27.2% (elevated O_3 ring 2,3 in 2000) (Fig. 11.1).

11.3.2. Exploratory statistical analysis

Pearson correlations between mean cross-sectional area and annual growing season 4th highest daily maximum 8-h average O_3 concentration were negative, signifying an inhibitory effect of O_3 on cross-sectional area growth (Table 11.1). The correlations for aspen clone 8L and white birch were not, however, statistically significant. WS was negatively and highly ($p = 0.000$) significantly correlated with mean cross-sectional area growth over the 5-year period in all aspen clones and in white birch (Table 11.1). Mean cross-sectional area was negatively correlated with PAR in aspen and birch. Only in aspen clones 8L, 42E, 216, and 259, however, was the correlation statistically significant. There was a tendency for mean cross-sectional area to be negatively correlated with

Table 11.1. Pearson correlations and their significance [r, (p =)] for mean cross-sectional area response and six predictor variables in five aspen clones and white birch

Species/clone	4th highest O_3[a]	WS[a]	GDD[a]	PAR[a]	SMC[a]	Precip.[a]
Aspen clone 8L	−0.070	−0.708	−0.156	−0.432	0.044	−0.189
	(0.713)	(0.000)	(0.411)	(0.017)	(0.816)	(0.318)
Aspen clone 42E	−0.505	−0.719	−0.129	−0.484	0.031	−0.170
	(0.004)	(0.000)	(0.496)	(0.007)	(0.872)	(0.370)
Aspen clone 216	−0.689	−0.725	−0.188	−0.389	0.007	−0.208
	(0.000)	(0.000)	(0.319)	(0.034)	(0.973)	(0.270)
Aspen clone 259	−0.422	−0.811	−0.305	−0.396	−0.009	−0.232
	(0.020)	(0.000)	(0.101)	(0.030)	(0.962)	(0.218)
Aspen clone 271	−0.535	−0.746	−0.215	−0.327	0.177	−0.243
	(0.002)	(0.000)	(0.253)	(0.078)	(0.348)	(0.195)
White birch	−0.246	−0.728	−0.177	−0.198	0.306	−0.321
	(0.190)	(0.000)	(0.349)	(0.295)	(0.100)	(0.083)

Note: WS = average growing season wind speed; GDD = seasonal growing degree days (heat units); PAR = growing season cumulative photosynthetically active solar radiation; SMC = biweekly averaged soil moisture content; Precip. = cumulative growing season precipitation.

[a]4th highest O_3 = growing season 4th highest daily maximum 8-h average O_3 concentration.

GDD and with precipitation, but only weakly. SMC was always positively correlated with mean cross-sectional area, but not significantly so (Table 11.1). SMC was not correlated ($p = 0.747$) with precipitation amount.

11.3.3. Evaluation of selected O_3 exposure indices

The frequency distribution of all growing season (1999–2003) hourly average O_3 concentrations in each of the three replicate elevated O_3 FACE rings is represented here by ring 2 (Fig. 11.2). Three-quarters of all growing season 4th highest daily maximum 8-h average hourly O_3 concentrations were $\leq$63 ppb (1999) or $\leq$60 ppb (2000–2003). In 1999, 95% of all O_3 concentrations were $\leq$84 ppb. During 2000–2003, 95% of all concentrations were $\leq$80 ppb. Over the 5-year period, 99.9% of concentrations were $\leq$100 ppb (1999) or $\leq$90 ppb (2000–2003) (Fig. 11.2).

The best performing (highest r^2 adjusted) O_3 exposure indices as single indicators of aspen cross-sectional area growth were growing season W126 (24 h) and growing season 4th highest daily maximum 8-h average O_3 concentration (Table 11.2). The dependence of cross-sectional growth on O_3 exposure calculated using W126 was statistically significant

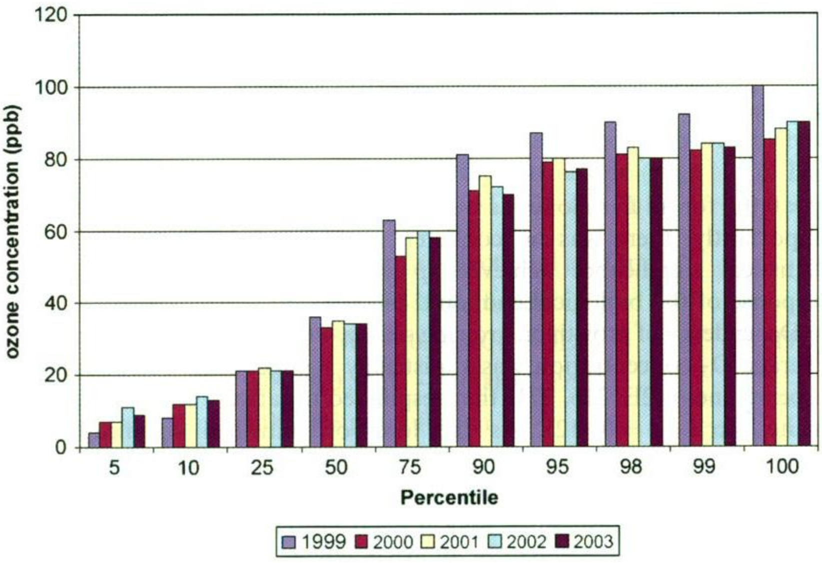

Figure 11.2. Frequency distribution of all 5-year (1999–2003) annual growing season hourly average O_3 concentrations (ppb) measured at the center of Aspen FACE elevated O_3 replicate ring 3.

Table 11.2. Evaluation of five O_3 exposure indices as single indicators of cross-sectional area growth in trembling aspen clones and white birch. Data are r^2 adjusted (*p* values) from cubic regression analysis of dependence of cross-sectional area growth (1999–2003) on growing season hourly average O_3 concentrations in three replicate elevated O_3 FACE rings

	Aspen clone					White birch
	42E	216	271	259	8L	
4th highest[a]	0.513	0.479	0.454	0.179	0.354	0.119
	(0.012)	(0.017)	(0.021)	(0.170)	(0.078)	(0.112)
SUM06[b]	0.170	0.137	0.163	0.223	0.228	0.031
	(0.180)	(0.217)	(0.187)	(0.130)	(0.160)	(0.251)
AOT40[c]	0.222	0.190	0.213	0.030	0.375	0.000
	(0.130)	(0.159)	(0.138)	(0.374)	(0.067)	(0.877)
Max 1 h[d]	0.250	0.314	0.197	0.121	0.371	0.331
	(0.109)	(0.069)	(0.152)	(0.236)	(0.069)	(0.015)
W126[e]	0.575	0.648	0.618	0.780	0.647	0.376
	(0.006)	(0.002)	(0.003)	(0.000)	(0.006)	(0.009)

Source: Modified from Percy et al. (2007).
[a]Growing season 4th highest daily maximum 8-h average O_3 concentration (ppb).
[b]Threshold-based sum of all daytime (08:00–19:59 h) ozone concentration hours $\geq$60 ppb (Lefohn and Foley, 1992).
[c]AOT-based sum of all growing season daytime (07:00–20:59 h; $>50\,W\,m^{-2}$) ozone concentrations $>$40 ppb (Fuhrer et al., 1997).
[d]Growing season maximum 1-h average ozone concentration (ppb).
[e]Growing season Weibull 126 concentration-weighted sum of 24 h average hourly ozone concentrations (Percy and Karnosky, 2007, Table 4). Multiple regression models of growing season 4th highest daily maximum 8-h average O_3 concentration, average growing season WS and GDD.

($p<0.01$) for all five clones as well as for white birch. However, and very importantly, there was no consistent association between the level of statistical significance achieved (*p* value) and the actual measured response of the biological endpoint.

Dependence of growth on growing season 4th highest daily maximum 8-h average O_3 concentration was statistically significant ($p<0.05$) for three aspen clones (42E, 216, 271) that responded negatively to O_3, but not for white birch ($p = 0.112$). As the level of statistical significance was consistent with measured response, calculation of O_3 exposure using the growing season 4th highest daily maximum 8-h average O_3 concentration resulted in a plausible biological association with response in the biological endpoint. Growth in all aspen clones and white birch was not dependent on O_3 exposure as calculated using the SUM06, AOT40 indices (Table 11.3). White birch growth was dependent ($p = 0.015$) on maximum 1-h average O_3 concentration, but growth in the aspen clones was not.

Table 11.3. Multiple linear regression model statistics for dependence of aspen clone and white birch cross-sectional area growth on growing season 4th highest daily maximum 8-h average O_3 concentration, average growing season WS, and growing degree days

Species/clone	Model significance	4th highest O_3 effect	4th Highest O_3 significance	R^2	4th highest O_3 (%)	R^2 adjusted
Aspen clone 8L	$p = 0.000$	Negative	$p = 0.900$	0.767	6.8	0.636
Aspen clone 42E	$p = 0.000$	Negative	$p = 0.001$	0.762	10.0	0.734
Aspen clone 216	$p = 0.000$	Negative	$p = 0.000$	0.894	47.4	0.882
Aspen clone 259	$p = 0.000$	Negative	$p = 0.038$	0.739	17.8	0.709
Aspen clone 271	$p = 0.000$	Negative	$p = 0.001$	0.757	28.6	0.729
White birch	$p = 0.000$	Negative	$p = 0.540$	0.615	6.0	0.570

Notes: 4th highest O_3 = growing season 4th highest daily maximum 8-h average O_3 concentration. % values indicate the percent contribution to the model.

11.3.4. Multiple regression models

Multiple linear regression models comprising the six indicator variables [growing season 4th highest daily maximum 8-h average O_3 concentration (4th highest O_3), GDD, WS, PAR, precipitation, and SMC] produced a best available fit (r^2 adjusted = 0.687–0.944) for the aspen clones and white birch. The highest value corresponded to aspen clone 216 (Eq. (11.1)). The lowest value corresponded to aspen clone 8L (Eq. (11.2)).

$$\begin{aligned}&\text{Clone 216 mean cross}-\text{sectional area (m}^2\text{)}\\&= 0.0130 - 0.000038\ \text{4th highest O}_3\\&\quad + 0.00022\ \text{WS} - 0.000001\ \text{GDD}\\&\quad - 0.000010\ \text{SMC} - 0.000002\ \text{PAR}\\&\quad - 0.000003\ \text{precipitation}\end{aligned} \tag{11.1}$$

$$\begin{aligned}&\text{Clone 8L mean cross-sectional area (m}^2\text{)}\\&= 0.00796 + 0.000026\ \text{4th highest O}_3\\&\quad - 0.0117\ \text{WS} + 0.000004\ \text{GDD}\\&\quad + 0.000007\ \text{SMC} - 0.000000\ \text{PAR}\\&\quad + 0.000002\ \text{precipitation}\end{aligned} \tag{11.2}$$

11.3.5. Best subsets regression

To balance this exceptionally high degree of goodness of fit against the practical utility requirements of our models, the best subset regression algorithm was systematically applied to the aspen clones and white birch. Best optimized models for the four aspen clones (42E, 271, 216, and 259) that responded negatively to O_3 within the range of 4th highest daily maximum 8-h average O_3 concentrations (62–96 ppb) measured during 1999–2003 in the six FACE rings were determined to be those comprising: (1) growing season 4th highest daily maximum 8-h average O_3; (2) average growing season WS; and (3) growing season GDD. Although the choice of 4th highest O_3, WS, and GDD cannot be considered the absolute best choice for the aspen clones and white birch, the models were highly statistically significant, had a very high goodness of fit (r^2 adjusted = 0.57–0.88), and were plausible from the biological point of view. The three-indicator (Eq. (11.3) for clone 216) model in the end was deemed considerably simpler, and easier to use in practical applications than the complete six-predictor model (Eq. (11.1)) listed earlier.

$$\begin{aligned}&\text{Aspen clone 216 mean cross-sectional area (m}^2\text{)}\\&= 0.00684 - 0.000031\ \text{4th highest O}_3\\&\quad - 0.00551\ \text{WS} + 0.000003\ \text{GDD}\end{aligned} \tag{11.3}$$

11.3.6. Ozone exposure–response models

We next developed a three-indicator multiple regression model as a tool for assessment of the impact of O_3 and two meteorological variables on trembling aspen and white birch cross-sectional area growth. For the aspen clones (271, 42E, 216, 259) that responded negatively to O_3, the corresponding r^2 adjusted ranged from 0.71 to 0.88 (Table 11.3). Regression coefficients at the growing season 4th highest daily maximum 8-h average O_3 concentration were negative and statistically significant ($p<0.038$) for aspen clones 42E, 216, 271, 259. Contribution of growing season 4th highest daily maximum 8-h average O_3 concentration was 10–47.4% of tree cross-sectional area growth, depending on relative sensitivity of the clone to O_3. The coefficients for 8L and white birch were not statistically significant (Table 11.3), implying that there was no negative effect resulting from O_3 exposure, or that exposure to O_3 resulted in some degree of growth stimulation.

11.3.7. Uncertainty in model prediction

The Monte Carlo method was used to randomly generate thousands of various scenarios of O_3, GDD, and WS based on the actual frequency distributions of these indictors measured at Aspen FACE during 1999–2003. Here, we use the example of aspen clone 271 to show the 95% confidence bands for the prediction of the growing season 4th highest daily maximum 8-h average O_3 concentration effect on mean cross-sectional area growth. At a given growing season 4th highest daily maximum 8-h average O_3 concentration, a vertical line can be drawn from the *x*-axis to the intersections with the red, green, and black lines. The black line intersection corresponds to the single midpoint prediction of the average (mean) cross-sectional area response to the given value of the growing season 4th highest daily maximum 8-h average O_3 concentration (Fig. 11.3).

Using the exposure–response models produced for the five aspen clones and white birch, we calculated the mean forecast (black line in Fig. 11.3) over a range of 60–95 ppb growing season 4th highest daily maximum 8-h average O_3 concentration. From a baseline of 60 ppb, the growth change predicted for aspen and birch as O_3 increases to 95 ppb is shown in Fig. 11.4. Among the five aspen clones, there was a clear difference in predicted outcomes. Clone 8L demonstrated a (+2.5% to +4.3%) growth stimulation with increasing O_3 to 90 ppb, followed by a –2.5%

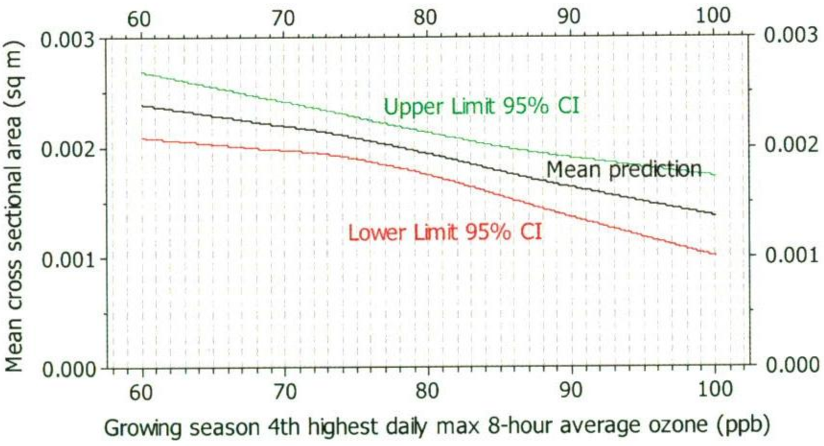

Figure 11.3. Exposure–response model (mean prediction ±95% confidence intervals) for effect of growing season 4th highest daily maximum 8-h average O_3 concentration on aspen clone 271 mean cross-sectional area growth.

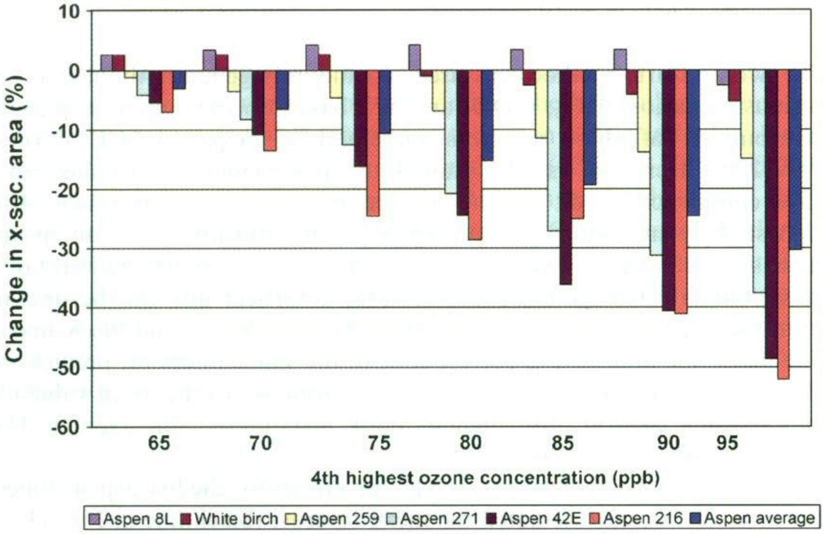

Figure 11.4. Percent change in aspen clone and white birch cross-sectional area from O_3 exposure at a growing season 4th highest daily maximum 8-h daily average O_3 concentration of 60 ppb at 5 ppb O_3 exposure increments. The response averaged across all five clones is also shown.

growth loss between 90 ppb and 95 ppb (Fig. 11.4). Between growing season 4th highest daily maximum 8-h average O_3 concentrations of 60 ppb and 65 ppb, predicted growth loss in decreasing order by clone was: clone 216, –7%; clone 42E, –5.41%; clone 271, –4.17%; clone 259, –1.15%. Relative to a growing season 4th highest daily maximum 8-h average O_3 concentration of 60 ppb, mean cross-sectional area growth at 80 ppb was predicted to have decreased by: clone 216, –28.5%; clone 42E, –24.3%; clone 271, –20.8%; clone 259, –6.9% (Fig. 11.4). Averaging negative (clones 42E, 271, 216, 259) and positive (clone 8L) responses across all five aspen clones, the change in growth between growing season 4th highest daily maximum 8-h average O_3 at 5 ppb increments was predicted to be: –3.0% (65 ppb); –6.5% (70 ppb); –10.7% (75 ppb); –15.2% (80 ppb); –19.3% (85 ppb); –24.6% (90 ppb); –31.1% (95 ppb).

White birch, like aspen clone 8L, exhibited growth stimulation to O_3 at lower concentrations followed by growth inhibition at higher O_3 concentrations. Birch cross-sectional area growth was predicted to be stimulated at growing season 4th highest daily maximum 8-h average O_3 concentrations of ≤ 75 ppb and reduced between –1.05% and –5.3% at growing season 4th highest daily maximum 8-h average O_3 concentrations ≥ 80 ppb (Fig. 11.4).

11.4. Discussion

We based our work on a hypothesis advanced by Krupa et al. (2003) "… that it should be possible to build an appropriate and inclusive predictive model comprising all important meteorological predictors plus soil moisture data that, together, would yield a first-order approximation of atmospheric O_3 flux and stomatal uptake." We also built upon the earlier approach of Hogsett et al. (1997) and used an important endpoint in a key species as recommended by Laurence and Andersen (2003). In so doing, we used a multi-year dataset from our randomized block, ecosystem-scale, free-air experiment to develop realistic exposure–response models based on a modified (growing season only) version of the United States (Federal Register, 2008) and Canadian (CCME, 2000) ambient air quality standard for O_3.

The aspen clones used in this study represented a wide range of sensitivity to O_3. They were originally selected based on foliar symptoms from some 220 clones representing 15 populations over the entire conterminous U.S. natural aspen range (Berrang et al., 1986) and later validated in field trials under conditions of varying ambient O_3 (Berrang et al., 1989; Karnosky et al., 2003b) and open-top chamber experiments (Karnosky et al., 1996, 2006). Both white birch and aspen clone 8L have been previously demonstrated to be very tolerant of O_3 at Aspen FACE over an 8-year growth cycle (Karnosky et al., 2003c, 2005). Our models confirmed their relative degrees of tolerance by predicting that aspen clone 8L growth was (Fig. 11.4) stimulated at growing season 4th highest daily maximum 8-h average O_3 concentrations <95 ppb. White birch growth was reduced, but only at growing season 4th highest daily maximum 8-h average O_3 concentrations >75 ppb. In demonstrating both positive and negative growth response, our exposure–response models conformed to the theory of hormesis. Calabrese (2005) has convincingly stated the case for the hormetic dose–response relationship as underlying the toxicological basis for risk assessment. It has been only rarely demonstrated to this point in time with O_3 exposure–plant response (Jäger & Krupa, 2008), possibly because of an overwhelming focus on identifying negative responses (Manning, 2005b).

Co-measured response and indictor variables for aspen and white birch yielded regression models that were statistically significant. Our initial seven meteorological growing season accumulated (GDD, PAR, precipitation) and averaged (WS, SMC) indicator data were derived from scan intervals of varying lengths. Our decision to delete RH from subsequent regression analysis was based on (1) its co-linearity with precipitation and (2) the fact that precipitation was added earlier in best subsets regression analysis. The resulting six-indicator variable multiple regression models provided a statistically very highly significant goodness of fit in terms of r^2 adjusted, regression ANOVA F-test significance, and performance relative to recorded productivity within the FACE rings. However, although they accounted for most of the variability in mean cross-sectional area growth, they were very complex and very data dependent. In addition, not all the variables (SMC, PAR) are routinely reported across the landscape and model utility would, thus, have been compromised. The three-indicator models identified in our best subsets regression had a high degree of goodness of fit, and should be very simple to use within a North American ambient air quality O_3 risk analysis context. The confidence bands can, in practice, be used by regulators to define uncertainty in the prediction.

We are aware that the intrinsic relationship between O_3 and tree growth is, of course, non-linear. Although multiple linear regression models of aspen clone growth on O_3 were very highly statistically significant, polynomial cubic regression (Millard & Neerchal, 2001) was used to evaluate whether the assumption of non-linearity in tree growth response to O_3 exposure could be verified. The resulting bivariate cubic curves (Percy et al., 2006, 2007) of tree cross-sectional area growth response to growing season 4th highest daily maximum 8-h average O_3 displayed a significant degree of curvature and an improvement in goodness of fit when compared with a simple bivariate linear model. However, although a non-linear model could slightly enhance goodness of fit and predictive power, it would certainly be less utilitarian. In other words, any increase in predictive power yielded by the more complex cubic regression model may not compensate for lowered ease of use by regulatory agencies (Percy et al., 2007).

The importance of WS as a factor in ambient O_3 formation (NRC, 1991) and O_3 flux through stomata (cf. Ashmore, 2004) is well known. In FACE systems, ambient air is used to dilute higher concentrations of emitted O_3 as the air stream is carried from outside the ring, into, and through the tree canopy. Ozone was fumigated in this experiment when WS measured at ring center was above $0.5\,\mathrm{m\,s^{-1}}$ and below $4.0\,\mathrm{m\,s^{-1}}$. It is interesting that the positive relationship of WS to O_3 sensitive clone 216 growth in the six-predictor model (Eq. (11.1)) was opposite to that (negative) in the final three-variable (Eq. (11.3)) model. The relationship of peak hourly to seasonal average O_3 concentrations (Karnosky et al., 2003c, 2005) within the elevated O_3 rings was quite consistent during the 5-year study period. Maximum 1-h average concentration was higher (106 ppb O_3 ring 3 in 1999) than in the succeeding years 2000–2003 ($<$93 ppb) (Fig. 11.3).

We did not have multi-port continuous monitoring data available for the FACE rings. This is being addressed through a planned intensive co-located active and passive monitoring study to more completely assess vertical and horizontal O_3 profiles within the tree canopy. However, we know from cumulative monthly exposure data collected by passive monitors that there was only a slight gradient in accumulated O_3 exposure within the core area of the elevated O_3 rings (Karnosky et al., 2007b) where growth measurements were taken. The pattern of these passive data did not seem to indicate a large influence of WS on O_3 concentrations, but rather, possibly the combined influence of mixing with distance and the influence of canopy uptake. If this hypothesis is indeed valid, and it has not been tested here, there seem to be some complex interactions related to WS that should be considered in future analysis.

In previously published analyses by Percy et al. (2007), four O_3 exposure indices were evaluated for their efficacy as single indicators of aspen and white birch cross-sectional area growth. This work concluded that the annual growing season 4th highest daily maximum 8-h average O_3 concentration was a much better single indicator of aspen growth than either SUM60, AOT40 or 1-h maximum O_3 concentration. Using the same dataset, we have now extended previous analyses to include the W126 sigmoidally weighted cumulative index developed by Lefohn and Runeckles (1987). As is evident from Table 11.2, with one exception (white birch, maximum 1-h average O_3 concentration), only growing season 4th highest daily maximum 8-h average O_3 concentration (aspen clones 271, 216, 42E) and W126 (aspen clones 271, 216, 42E, 259, 8L plus white birch) were statistically significant single growth indicators. The theory and application of the W126 index as developed by Lefohn and Runeckles (1987) has recently been succinctly summarized (Lefohn, 2006). The W126 is based upon a sigmoidal weighting function that (1) focuses on hourly average concentrations as low as 40 ppb; (2) has an inflection point near 65 ppb; and (3) has an equal weighting of 1 for hourly average concentrations $\geq$100 ppb. For any hourly average O_3 concentration, that concentration is multiplied by the corresponding sigmoidal weighting value and then all concentrations are summed (Lefohn, 2006). The frequency distribution (Fig. 11.2) of hourly average O_3 concentrations in this manipulative study resulted in a greater relative weight assigned to approximately 20% of the O_3 concentrations that were at or above the designated W126 inflection point of 65 ppb. This weighting may have unduly enhanced the mathematical relationship between W126 O_3 exposure and response of the biological endpoint. Pearson correlation analysis had previously indicated that there was no statistically significant relationship between O_3 exposure (growing season 4th highest index) and aspen clone 8L ($p = 0.713$) or white birch ($p = 0.190$) cross-sectional area growth (Table 11.1).

There is a continued desire on the part of air quality regulators to move toward a "biologically based standard" to protect vegetation (US EPA, 2006). At this time, it is unclear why the W126 was a statistically significant single indicator of aspen and birch growth. To evaluate the biological relevance of the W126 index statistical significance, we compared, measured, and modeled growth responses. Our conclusion from this analysis is that the W126 index greatly overestimated the negative responses for aspen clones 8L ($p = 0.006$), 259 ($p = 0.000$), and white birch ($p = 0.009$) (Table 11.2). This is further supported by the lack of a statistically significant contribution from O_3 exposure to aspen 8L ($p = 0.900$) and white birch ($p = 0.540$) growth (Table 11.3). Aspen clone 8L and white birch have clearly been documented to be positively affected by O_3 (Karnosky et al., 2005; King et al., 2005; Kubiske et al., 2006). In the case of white birch, this may be partly due to a competitive advantage conferred by its greater tolerance to O_3 relative to its planted cohort, aspen clone 216. Aspen clone 259 in open-top chamber experiments has been considered to be highly O_3 sensitive (Karnosky et al., 1996). However, when inter-planted with other aspen clones, clone 259 manifested very high rates of mortality within the O_3 rings during the first two fumigation seasons (1998–1999). There is, of course, the possibility that the only most tolerant individuals within clone 259 were left to be measured during 1999–2003, and, therefore, any modeled estimates for this one clone may have been biased. In summary, at least for our data in this analysis, the "statistical fit" achieved by the W126 O_3 exposure index certainly does not reflect the "biological fit" based on measured response.

The growing season 4th highest daily maximum 8-h average O_3 concentration index does not include a weighting function and, thus, may not be as influenced as W126 by exposure frequency distribution at our lower O_3 site over the 5-year period. Rather, it may be more influenced more by the relative difference between peak and average concentrations. The fact that the growing season 4th highest daily maximum 8-h average O_3 concentration was a statistically significant indicator of growth only in aspen clones that responded negatively to O_3 during the life of the experiment is important. This fact appears to confer greater biological plausibility on it, than on the W126.

On the basis of our data, in terms of potential index application within a secondary (welfare-based) standard should it ever be promulgated, the 4th highest daily maximum 8-h average O_3 concentration (1) appears to have greater association than the W126 O_3 exposure index with an economically and ecologically relevant biological endpoint (growth) for two widely distributed and important northern hardwood species and (2) has the advantage of requiring only a change in averaging time (to annual) and perhaps a slight change in form. The current primary NAAQS form (Federal Register, 2008) actually requires data from only the 2nd and 3rd quarters of the year (the "ozone season"). It is important to note that the growing season 4th highest daily maximum 8-h average O_3 concentration indicator used in our models in fact represents the *biologically relevant* portion of the NAAQS (Federal Register, 2008) and CWS (CCME, 2000).

11.5. Conclusions

We have developed regression-based O_3 exposure tree response models comprising annual growing season 4th highest daily maximum 8-h average O_3 concentration, accumulated GDDs, and average WS. The models predict extremely well within a wide range of 4th highest daily maximum 8-h average O_3 concentration and have immediate relevancy to ambient exposure conditions experienced by two of North America's most widely distributed tree species. The models are highly statistically significant, have a high degree of goodness of fit, are endpoint based, and should be simple to use within the North American context. The models include defined limits of uncertainty in prediction as required for risk analysis.

Our data document that O_3 exposure may result in both positive and negative growth responses in aspen and birch that conform to the theory of hormesis. Aspen clone 8L and white birch modeled and measured 5-year growth responses to O_3 exposure in the ambient air context conformed to the theory of hormesis, or low dose stimulation followed by higher dose inhibition. Comparative evaluation of five O_3 exposure indices demonstrated that the W126 index greatly overestimated the negative response to O_3 and that the growing season 4th highest daily maximum 8-h average O_3 concentration index has high statistical significance and a much greater association with the biological endpoint.

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